Global analysis of depletion and recovery of seabed biota after bottom trawling disturbance

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Bottom trawling is the most widespread human activity affecting seabed habitats. Here, we collate all available data for experimental and comparative studies of trawling impacts on whole communities of seabed macroinvertebrates on sedimentary habitats and develop widely applicable methods to estimate depletion and recovery rates of biota after trawling. Depletion of biota and trawl penetration into the seabed are highly correlated. Otter trawls caused the least depletion, removing 6% of biota per pass and penetrating the seabed on average down to 2.4 cm, whereas hydraulic dredges caused the most depletion, removing 41% of biota and penetrating the seabed on average 16.1 cm. Median recovery times posttrawling (from 50 to 95% of unimpacted biomass) ranged between 1.9 and 6.4 y. By accounting for the effects of penetration depth, environmental variation, and uncertainty, the models explained much of the variability of depletion and recovery estimates from single studies. Coupled with large-scale, high-resolution maps of trawling frequency and habitat, our estimates of depletion and recovery rates enable the assessment of trawling impacts on unprecedented spatial scales.

logistic recovery model | systematic review | metaanalysis | impacts | trawling

Fisheries using bottom trawls are the most widespread source of anthropogenic physical disturbance to global seabed habitats (1, 2). Almost one-quarter of global seafood landings from 2011 to 2013 were caught by bottom trawls (3). Development of fisheries, conservation, and ecosystem-based management strategies requires assessments of the distribution and impact of bottom trawling and the relative status of benthic biota and habitats. There are many drivers for such assessments, including (*i*) policy commitments to an ecosystem approach to fisheries, (*ii*) requirements to take account of trawling impacts in fisheries and environmental management plans, (*iii*) demands from certification bodies to assess fisheries' environmental impacts, and (*iv*) the need to evaluate the effects of alternate management measures to meet conservation and management objectives (4–6). These assessments are used to assess the sustainability of bottom trawl fisheries, formulate priorities for habitat protection, and ultimately, achieve a balance between fisheries production and environmental protection. The distribution of bottom trawling is increasingly well-characterized by vessel tracking and other monitoring systems (7), but impacts depend on the magnitude of trawling-induced mortality and recovery rates of biota, for which the current evidence base is incomplete, dispersed, and often contested (4, 8).

Bottom trawls [here defined as any towed bottom-fishing gear, including otter trawls (OTs), beam trawls (BTs), towed (scallop) dredges (TDs), and hydraulic dredges (HDs)] are used to catch fish, crustaceans, and bivalves living in, on, or above the seabed (9). Bottom trawling resuspends sediments (10, 11); reduces topographic complexity and biogenic structures (12–14); reduces faunal biomass, numbers, and diversity (15, 16); selects for communities dominated by fauna with faster life histories (17); and produces energy subsidies in the form of carrion (18). These effects lead to changes in community production, trophic structure, and function (19, 20). Given the patchy and dynamic distribution of bottom fishing (21), fished seabeds comprise a mosaic of undisturbed, recently impacted, and recovering benthic communities and habitats (22). The state of each patch within this mosaic depends on the history and frequency of past trawling impacts and the recovery rates of the biota present (23).

Recovery rates after trawling depend on recruitment of new individuals, growth of surviving biota, and active immigration from adjacent habitat. Most existing estimates of recovery rates come from experimental studies, with changes in abundance recorded before and after experimental trawling (15, 16). Although these experiments provide reliable estimates of immediate mortality, their small scale is likely to underestimate recovery time, in particular for mobile fauna. This underestimation is because immigration makes a greater contribution to recovery when biota are relatively more abundant around

Significance

Bottom trawling is the most widespread source of physical disturbance to the world's seabed. Predictions of trawling impacts are needed to underpin risk assessment, and they are relevant for the fishing industry, conservation, management, and certification bodies. We estimate depletion and recovery of seabed biota after trawling by fitting models to data from a global data compilation. Trawl gears removed 6–41% of faunal biomass per pass, and recovery times posttrawling were 1.9–6.4 y depending on fisheries and environmental context. These results allow the estimation of trawling impacts on unprecedented spatial scales and for data poor fisheries and enable an objective analysis of tradeoffs between harvesting fish and the wider ecosystem effects of such activities.

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the impacted site and because most experiments have been conducted in infrequently and untrawled areas (16). On fishing grounds, impacts occur on larger scales, such that untrawled and infrequently trawled areas become scarce when there is more trawling activity. Furthermore, experiments typically focus on recovery after single trawling events rather than recovery from successive events typical of fishing grounds.

The development of satellite-based vessel monitoring systems has enabled scientists to map commercial fishing activity at high resolution (7). Such maps have been used to design studies of the comparative impacts of towed bottom-fishing gears across gradients of commercial fishing frequency (herein equals comparative studies). In contrast to experimental studies, these studies account for the spatial extent, frequency, and temporal variability in fishing activity and are expected to provide more representative estimates of recovery rates. When these estimates are coupled with estimates of the mortality of biota from experimental studies, they can be used to assess the status of impacted biota on fishing grounds. Presently, there are too few studies to adopt the alternative approach of analyzing large-scale studies directly recording recovery from trawling (24).

We used the logistic growth equation (25) to describe recovery of benthic fauna, because it provides an effective abstraction of the complex recovery dynamics of populations and communities and can be fitted to available data (22, 23, 26). This model is identical to the Schaefer models commonly used in fisheries management when the data to implement full age or size-structured models are not available (27). If we assume that the recovery of biomass or numbers (hereafter abundance) of biota B after trawling is described by the logistic growth equation, then the equilibrium solution can be used to estimate B as a fraction of carrying capacity K in an environment subject to chronic fishing disturbance (28):

$$\frac{B}{K}=1-F\frac{d}{r}, \qquad [1]$$

where F is trawling frequency, d is the depletion of biota caused by each trawl pass (expressed as a proportion), and r is rate of increase interpreted here as the recovery rate. Eq. **1** only requires estimates of F, d , and r to estimate relative abundance B/K (28). Eq. **1** suggests that r is constant, but in communities composed of species with a range of r values, trawling selects for species with faster life histories that are more resilient, and therefore, r can be expected to increase with F. We found that the relationship between community B/K and F for communities is well-approximated by a log-linear relationship (*SI Appendix*). We, therefore, estimated r at F = 0 and assuming a log-linear relationship between B/K and F (Eq. **2**). More sophisticated models of recovery can account for differential responses of groups with contrasting life histories and other aspects of community dynamics and thus, provide a better description of underlying processes (19, 29), but higher parameter demands limit their application to systems with a substantial amount of available data. Conversely, if d and r can be estimated and if associated uncertainties can be quantified, the logistic model would facilitate assessment of trawling impacts in most marine systems. Different gears and substrata will have different levels of seabed contact or penetration, and these factors will influence d. Penetration depth is, however, largely independent of the towing speed (6). If a strong relationship exists between the penetration depth and d, this relationship can be used to obtain estimates of depletion for trawl gears for which no empirical depletion estimates are available. Trawling frequency F is defined as the swept area ratio, which is the area trawled annually divided by the studied area (kilometers^2 kilometer^{-2} year^{-1}; simplified to year^{-1}); it should ideally be calculated for small cells (~1 km^2), because trawling tends to be spatially clustered at larger scales.

Here, we conduct a metaanalysis of experimental studies of trawling impacts to estimate depletion of biota after trawling. We report the effect on the abundance of whole benthic macroinvertebrates communities, including infauna and epifauna. We combine this with a metaanalysis of results from large-scale comparative studies of trawling effects on fishing grounds to estimate recovery rates of seabed biota and describe how they vary with gear characteristics and environment. All data were collated from studies that were quality assured after systematic review methodology, thereby avoiding selection bias (30).

Results

Twenty-four comparative and 46 experimental studies met the criteria for inclusion in our analyses (*SI Appendix*, Tables S1–S3). Studies were mostly temperate and concentrated in northwestern Europe and the northeastern United States (Fig. 1). None of the studies that met the criteria examined the effect of trawling on biogenic habitats, but there were sufficient studies in other habitats. Many gear–habitat combinations were not represented in the studies reviewed, because many fishing gears are only suitable for fishing on particular seabed types or species associated with those habitats (*SI Appendix*, Table S1) and because some habitats are less widespread than others (7).

Depletion rates estimated from the experimental studies for biomass and numbers were not significantly different. Thus, the pooled estimates of d (*SI Appendix*, Table S4) apply to both biomass and numbers. Estimates of depletion d and penetration depth P by gear type were very closely correlated (Fig. 2) (Pearson's r = 0.980, P = 0.020). OTs had the smallest impact, removing on average 6% of organisms per trawl pass and penetrating on average 2.4 cm into the sediment. Median penetration depths were 2.7 and 5.5 cm for BTs and TDs, respectively, and the corresponding median depletions per trawl pass were 14 and 20%, respectively. HDs had the largest impact, removing on average 41% of organisms per pass and penetrating 16.1 cm.

The effect of trawling frequency on relative biomass estimated from the comparative studies showed a log-linear relationship, with each unit increase in swept area ratio linked to a mean fall in biomass of 15.5% (Fig. 3*A*). None of the other environmental variables significantly affected this response (Table 1). The effect of sediment composition on community biomass depletion was not significant (Table 1, community biomass and *SI Appendix*,

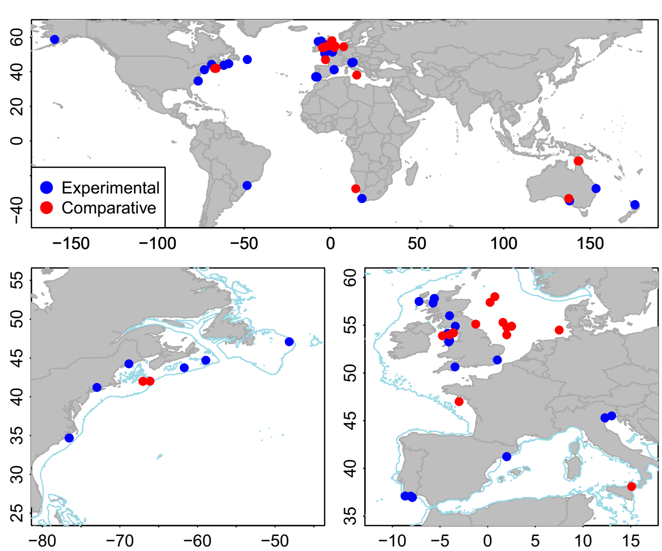

Fig. 1. Maps of the locations of the studies. The higher-resolution maps of the northwest and northeast Atlantic give more detail for two areas with high concentration of studies. The 200-m depth contour is shown in blue.

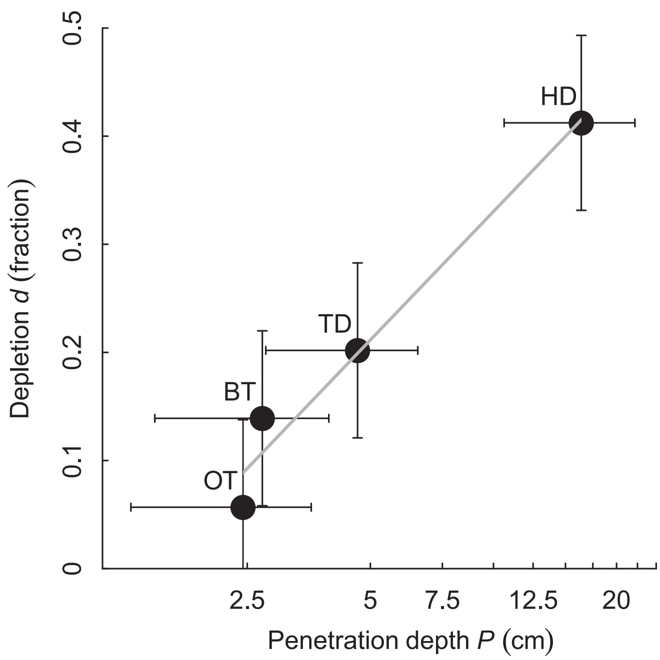

Fig. 2. The relationship between the penetration depth P and depletion d of macrofaunal community biomass and numbers caused by a single trawl pass for different trawl gears (means ± SD).

Table S5), but the model estimates for gravel are nevertheless shown in Table 1 for community biomass to allow comparison with the significant effects of gravel found for community numbers (Table 1, community numbers and *SI Appendix*, Table S5). Mean community r (estimated using *SI Appendix*, Eqs. **S4.1** and **S4.2** from d and b) increased with trawling frequency from 0.82 y^{-1} when there was no trawling (5–95% uncertainty intervals = 0.42–1.53) to 1.73 (0.89–3.23) y^{-1} when the trawling frequency was 10 y^{-1} (using the mean estimated d across gears OT, BT, and TD; d = 0.13) (*SI Appendix*, Fig. S1 and Table S6). The increase in r, which results from changes in community composition to favor biota with faster life histories, is, therefore, relatively slight across ranges of trawling frequencies that dominate those on real fishing grounds (e.g., 0–1 y^{-1}) (7, 31, 32). The r estimate of 0.82 y^{-1} enables estimates of median time to recovery (T) to 0.95K for a range of levels of depletion (Fig. 3*B*). For example, if the fraction depleted D = 0.5K, then recovery time is 3.6 y (5–95% uncertainty intervals = 1.9–6.4 y).

The effect of trawling on community numbers, estimated from the comparative studies, increased significantly with the gravel content of the sediment (Fig. 3*C*, Table 1, community numbers, and *SI Appendix*, Table S5), and this effect persisted when examined among gears. The reductions in benthic community numbers for each unit increase in trawling frequency were 3.1% at 0% gravel content (typical for BT studies), 5.5% at 1% gravel content (typical for OT studies), and 72% at 45% gravel content (typical for TD studies). The estimates of r for community abundance range from 0.18 y^{-1} for TD on 45% gravel to 4.47 y^{-1} for BT on 0% gravel, with high uncertainty. These r estimates result in a median recovery time T from 0.5K to 0.95K of 0.7–16.6 y (Fig. 3*D*). Other than gravel content, the inclusion of the ratio of d over primary production also resulted in reduced Akaike information criterion (AIC) compared with the model with no additional explanatory variables, with the effect of trawling on numbers increasing with d and decreasing at higher levels of primary production (Table 1, community numbers and *SI Appendix*, Table S5).

Discussion

This study is an attempt to quantify the impacts of bottom trawling and recovery of seabed biota by synthesizing data from trawling studies after a systematic review of the available evidence base. We developed a method to derive the recovery rates of benthic macrofaunal invertebrate communities from trawling by combining results from experimental and comparative studies and provide estimates of depletion and recovery, including a quantification of uncertainty

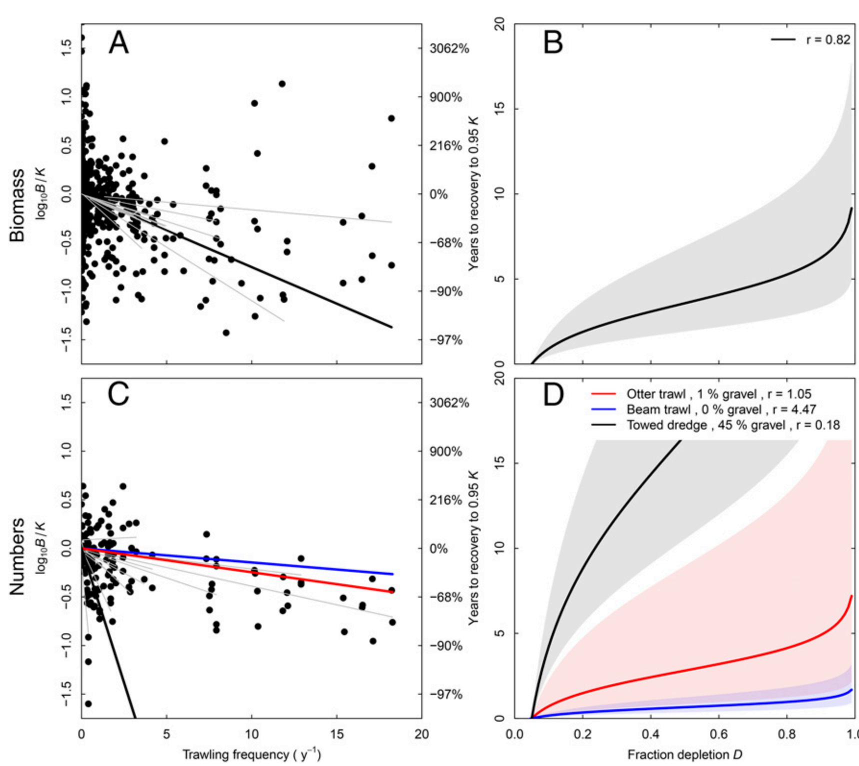

Fig. 3. The relationship between trawling frequency and total community (*A*) biomass and (*C*) numbers. The thicker lines are the fixed effects, and grey lines are the random effects of the individual studies (not all visible, because many studies had small ranges and low trawling frequencies). Recovery time to 0.95K for depleted total community (*B*) biomass and (*D*) numerical abundance as a function of estimated r and initial depletion D. In *A* and *B*, lines are the median estimate based on the mean d across all gears. In *C* and *D*, lines are the median estimates for three different gear types based on the mean gravel content in the areas where studies using these gear types were carried out. The shaded areas indicate the 5–95% uncertainty intervals for estimates.

Table 1. Linear mixed model (*SI Appendix*, Eq. S3.1) fits for the analysis of data from comparative studies of changes in biomass and numbers

Model	Slope (*b*)	SE	df	*t* Value	*P* value	AIC
Community biomass						
TF	−0.07522	0.0158	503	−4.732	<0.0001	566.9
TF	−0.07142	0.0172	502	−4.148	<0.0001	568.4
TF: gravel	−0.00067	0.0010	502	−0.648	0.5168	
TF	−0.08623	0.0325	502	−2.653	0.0082	568.8
TF: *d*/PP	125.6879	373.7966	502	0.336	0.7368	
Community numbers						
TF	−0.21185	0.1342	141	−1.577	0.1169	89.5
TF	−0.01451	0.0942	140	−0.153	0.8778	81.1
TF: gravel content	−0.01206	0.0035	140	−3.377	0.0009	
TF	0.25300	0.2145	140	1.048	0.2964	86.1
TF: *d*/PP	−6,892.96900	2,676.5453	140	−2.575	0.0111	

For community biomass, the model with the lowest AIC included no explanatory variables other than trawling frequency, but for community abundance, both gravel content and *d*/PP improved the AIC in relation to a model without other explanatory variables. Results for these variables are given under community biomass for comparative purposes. *d*, Depletion estimate from experimental studies (fraction per trawl pass) (*SI Appendix*, Table S4); gravel, sediment composition in percentage by weight; PP, primary production (milligrams C meter^{-2} day^{-1}); TF, trawling frequency.

based on all available data. The method for estimating the recovery rate from comparative studies is unique. Given that realistic and robust *r* estimates have been largely unavailable previously, this work is critically important. Recovery rates were estimated from changes in the biomass and numbers of biota across fishing grounds, and therefore, estimates are likely applicable to trawled shelf seas in general (at least in temperate waters where most of the studies were carried out). Our estimates of depletion and recovery enable the parameterization of models to predict the state of the benthic biota as a function of trawling frequency and levels of primary production and percentage gravel (28). Coupled with the emergence of large-scale estimates of trawling frequency (7), these models will support assessment of trawling impacts on unprecedented spatial scales, because our approach provides a quantitative estimate of status with minimal data requirements (28). The method is widely applicable, because it requires relatively few data inputs and could be applied worldwide, including for fisheries where trawl impacts remain unassessed. The *r* and *d* values that we estimate here with a broad geographic basis are based on the full body of available evidence and therefore, the most robust estimates available. The generality of our approach means that the outputs of assessments are accurate when averaging over larger scales but that biases may exist when used for local assessments. These results have global policy relevance for conservation and food security policy development, because they enable an objective analysis of the efficacy of different methods of harvesting food from the ocean to be considered in the light of the wider ecosystem effects of such activities on the marine environment. The results enable managers to understand the variable resilience of benthic systems to trawl fisheries and set limits of fishing accordingly.

Most continental shelves consist of relatively small intensively trawled areas, where the trawling frequency is in the range of 1–10 y^{-1}, and extensive infrequently trawled areas, where the trawling frequency is <1 y^{-1} and predominantly <0.25 y^{-1} (7). Our results show that trawling frequencies of 1 y^{-1} cause average declines of 15.5% in the biomass of benthic biota. Communities on gravel may be more sensitive to trawling, because they, on average, have a larger proportion of larger, long-lived, and sessile epifauna (33) that are particularly sensitive to trawling (34). Effects were greater for gears that kill a larger fraction of the biota (larger d), because they penetrate the sediment more deeply and weaker in areas of higher primary production, where higher food supply to the benthos may result in a higher recovery rate.

The ranking of different fishing gears with respect to their magnitude of impact reported here is similar to the ranking in previous metaanalyses of small-scale experimental studies (15, 16), although our estimates of *d* are smaller, probably because we adjusted for the number of trawl passes, whereas previous analyses did not. The use of depletion to primary production ratio as a proxy for community resilience to trawling has the advantages of being easily understandable and easy to estimate for new areas and fisheries. The ratio of depletion over primary production might support rapid preliminary large-scale risk assessments of potential trawling impacts on community abundance to guide more region-specific studies. The close relationship between penetration depth and depletion can be used to estimate depletion resulting from the pass of a given trawl gear when no direct depletion estimate is available. Accurate estimates of penetration depth are much easier and cheaper to obtain than estimates of depletion, would support preliminary impact assessments by gear type, and can even be generated using numerical models (11).

Our analyses did not identify any variables other than trawling frequency that affected community biomass. This finding is surprising given the contrasting results for numbers and that some comparative studies and past metaanalyses of experimental studies have shown interaction effects between gear type and habitat type (16, 29). The relatively small number of studies included in the biomass analysis and the high variability associated with benthic sampling, which cannot be fully controlled in a metaanalysis, may have contributed to this discrepancy. Our results for biomass imply that a single estimate of recovery rate *r* is appropriate when assessing impacts on the different habitat types studied here. They also suggest that differences in time to recovery and expected biomass (*B/K*) will be driven primarily by gear type (and hence, d) and trawling frequency (F).

Our estimates of biomass recovery times are similar to empirical measurements of recovery taken in three areas where commercial trawling was stopped (4–5 y) (24) but longer than estimates from small-scale experimental studies, which are on the order of 25–500 d (15, 16). The scale dependency of recovery times has important implications for management, because recovery will be faster when trawled areas are closer to less impacted areas from which individuals can recruit or migrate (as also shown in ref. 22). We found that biomass recovery rates were slower and that recovery times were longer than those for numbers. This result is expected based on the population dynamics of seabed biota. Recovery in numbers is driven more strongly by recruitment than recovery of biomass, which is driven by increases in the size and age structure of the population through growth of individuals. We recommend the use of recovery rates for community biomass when modeling trawl impacts and their consequences. This approach will give due weight to recovery of body size and age structure as well as numbers and take account of energy flow through food webs and other ecosystem processes that are linked closely to biomass. Recovery times as estimated from the logistic model nevertheless do not imply that the communities will recover over these times to the species, size, and age composition that existed before trawling, but they do imply the recovery of total biomass or numbers and related cross-species ecosystem processes, such as aggregate secondary production.

Uncertainties around mean/median estimates of penetration depth, recovery, and depletion were high, despite the careful screening of included data (which also decreased the sample size and potentially, power to detect effects) (30). However, our approach allows us to address directly some aspects of uncertainty, and the broad distribution of resulting depletion and recovery estimates show that large site-specific differences in the response of seabed communities to trawling are expected. The advantage of characterizing uncertainty is that it can be propagated in future risk and impact analyses. Given the unexplained variance in r, percentiles from the distribution of plausible values might be selected to reflect the degree of risk aversion in the management system. The extent of risk aversion is a nonscientific decision (although it would be informed by science) that would likely be made by managers and other stakeholders. Risk aversion would likely depend on the perceived value of a habitat type. A risk-averse approach might adopt a value of r from a lower percentile of the distribution (e.g., the 10 or 25%) rather than the median (*SI Appendix*, Table S6 shows a selection of values).

Our use of comparative studies provides improved estimates of recovery compared with those from previous small-scale experiments studies, because they are based on larger-scale measurements from fishing grounds. Comparative studies may, however, be affected by "shifting baselines" (35), where historical trawling has removed the most sensitive organisms and only resilient organisms remain. Because trawling selects for species with faster life histories that are more resilient, recovery time will increase with trawling frequency. Our finding that mean community r increases with F conforms with previous observations of shifts toward species with faster life histories in disturbed communities (36). This effect is apparent across a range of plausible trawling frequencies from >0 to 10 y^{-1} but would be small for the great proportion of most fishing grounds, where swept area ratio is less than 1 y^{-1} (7). Although this shift means that previously trawled communities may be more resilient to additional trawling, it does not mean that they will recover any faster to the original pre-trawling state. For this reason, we used the r estimate of untrawled communities for estimating recovery times. Selective effects linked to trawling history are likely to be strongest for long-lived sessile epifauna that build biogenic reefs, such as sponges and corals. The estimates of r and T presented here are applicable to invertebrate communities living in sedimentary habitats but not biogenic habitats, because no studies of trawling impacts on biogenic habitats met the rigorous selection criteria imposed by the systematic review.

In summary, we apply widely applicable methods to estimate depletion and recovery rates of benthic invertebrate communities after trawling. By accounting for the effects of gear type and penetration, environmental variation, and uncertainty, our analysis explained much of the variability of depletion and recovery estimates from single studies. Coupled with large-scale, high-resolution maps of trawling frequency and habitat, our estimates of depletion and recovery rates will enable analysis of trawling impacts on unprecedented spatial scales to inform best practices to achieve sustainable fishing and will be of use to policymakers, conservation planners, and fisheries managers for risk assessment and the evaluation of management strategies.

Methods

We present analyses for whole-community biomass and numbers of benthic invertebrates. Changes in the abundance of seabed biota after trawling depend on the mortality caused by each pass of a trawl and the rate of recovery of the biota between trawl passes. We estimated the immediate depletion of biota (d) caused by a trawl pass from a metaanalysis of experimental studies of trawling impacts. We estimated the recovery rates (r) of biota from a metaanalysis of comparative studies of trawling impacts. The analyses were structured to assess the effects of gear type, penetration depth, and environmental variables (e.g., depth and sediment composition) on depletion and recovery.

Depletion. Depletion was estimated using data collated from experimental studies of trawling impacts identified using systematic review methodology. A comprehensive literature search of journal papers, book chapters, and grey literature reports was carried out. Details of literature search terms, databases, and study inclusion criteria are provided in the systematic review protocol by Hughes et al. (30). All included studies quantified the immediate mortality of biota after one or multiple trawling events. Each identified study had to pass quality assurance criteria before data from the study were included in the collated dataset.

We classified gear types as OTs, BTs, TDs, or HDs (*SI Appendix*). The reduction in abundance of biota resulting from one pass of a trawling gear depends on the characteristics and operation mode of the gear. Different gears are designed to have different levels of seabed contact or penetration depending on the target species and seabed type, and these factors will influence mortality (37). Consequently, we assessed the relationship between mortality and penetration depth of the gear. Some of these studies were conducted in previously trawled areas with a lowered abundance of biota, but because we are estimating the fraction of organisms removed rather than the absolute amount, we expect that this will have had little effect on our estimates of d. Depletion d was estimated using a generalized linear mixed model implemented in the package nlme in R (38, 39), with the log of the ratio of the biomass or abundance in trawled over untrawled areas (*lnRR*) as the response variable, $\log_2$ (time t in days since trawling) and gear type as fixed factors, and the study as a random effect assuming a Gaussian error distribution. We weighted *lnRR* values by the inverse of their variance, which is normal practice in metaanalyses. We estimated d as the intercept for the different gears at $t = 0$.

Predicted penetration depth of each gear type into the seabed was estimated from values in the literature by averaging the reported penetration depths of the individual components of the gear (e.g., doors, sweeps, and bridles of an OT) weighted by the width of these components (details are in *SI Appendix*).

Recovery. Recovery rates were estimated using data collated from comparative studies of trawling impacts. All included studies sampled the biomass or numbers of whole communities of benthic invertebrates at two or more sites subject to different trawling intensities on commercial fishing grounds. Contributing studies were identified following the same procedure as for experimental studies (*SI Appendix*). In the analyses of the comparative studies, we assume that both K and observed gradients of trawling effort were unrelated to other environmental drivers and that the observed state of the biota is in equilibrium with the reported trawling effort. Gradients in trawling effort may be driven by regulation and seabed obstructions but are also observed in areas of homogenous habitat (29). Spatial patterns of trawling effort are also shown to be relatively stable over time in the few fisheries where high-resolution time series have been analyzed (40). K could vary across the trawl grounds because of environmental variations, and this source of variation will increase the uncertainty around relationships between B and F.

In the comparative studies, conversions between units of abundance were not always possible (e.g., biomass per unit sediment volume could not be converted to biomass per unit sediment area given sampling gears with different but unknown efficiencies), and therefore, absolute B or K could not be estimated. We normalized the data by expressing relative biomass or numbers as the B/K ratio and used a log-linear approximation for the relationship between community B/K and F:

$$\log_{10}\left(\frac{B}{K}\right) \sim b\,F, \qquad [2]$$

where b is the slope of the relationship (derivation taking account of the log-linear relationship between B/K and F and the distribution of trawling is in *SI Appendix*). After fitting a linear relationship to $\log_{10}B$ vs. F for each comparative study, K was estimated as the $10^{\text{intercept}}$ of this relationship.

The data collated from comparative studies were initially used to estimate relative changes in abundance (B/K) as a function of trawling frequency F. This approach differs from the aforementioned analyses of depletion, because the change in abundance with trawling is a response to both depletion (per trawl pass) and recovery. Because $b = d/r$ (Eq. **1**), after d is estimated from experimental data, recovery rate r can be estimated from the slope b of Eq. **2** after taking account of the log-linear nature of this relationship, which implies that r increases with F. To propagate uncertainty in the estimates of b and d into the estimate of r, we sampled the distributions of b and d estimates to derive the distribution of r (*SI Appendix*). Time to recovery from a given level of depletion D to a defined proportion ϕ of K at which recovery is deemed to have occurred (e.g., 0.95) was derived from the approach of Lambert et al. (22) (*SI Appendix*). When reporting recovery times, we report recovery from 0.5K to 0.95K.

Variables That Determine the Effect of Trawling in Comparative Studies. The effect of trawling on seabed biota in comparative studies could be influenced by different variables. Thus, we evaluated the explanatory power of several potential factors by including them as covariates in a linear mixed model (39) based on Eq. **2** and selecting the most parsimonious model using AIC. According to Eq. **2** the community response to trawling in $\log_{10}$ scale is approximately proportional to F, with slope a function of the ratio of d/r. The fixed part of the mixed models was, therefore,

$$\log_{10}(\text{Response}) \sim \text{Trawling frequency} + \text{Trawling frequency} \times \text{other variables},$$

where the response variable is community biomass or numbers and the "other variables" can be covariates for d, r, or their ratio (4). The intercept

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was removed, because $\log_{10}(B/K)$ with no impact = 0. We modeled "study" as a random effect, allowing the slope to vary per study. This approach accounted for the nonindependence of observations within a study. We checked the assumptions of the linear mixed model by visual inspection of the normalized residuals (38).

We expected that factors that lead to a higher *d* would strengthen the effect of trawling (e.g., higher penetration depth), whereas factors that lead to a higher *r* by affecting growth rates of individuals and populations (higher flow of energy to the seabed because of a higher production, shallower depth, or higher temperature) would weaken the effect. The closely related penetration depth *P* (continuous) and gear type (categorical) were examined as covariates for *d*. The following covariates for *r* were examined: primary production estimated from the vertically generalized productivity model (milligrams C meter^{-2} day^{-1}) (41) and particulate organic carbon flux to depth (grams C_{org} meter^{-2} year^{-1}) (42) as proxies for energy availability, mean sea bottom temperature calculated from monthly mean bottom temperature for 2009–2011 provided in MyOcean Product (GLOBAL-REANALYSIS-PHYS-001–009), depth (from GEBCO if not reported in the original study), habitat type, and sediment composition (gravel, sand, and mud content). Habitat types were classified as biogenic habitats, gravel, sand, muddy sand/sandy mud, and mud. Sediment gravel, sand, and mud content were extracted from the source studies by converting the sediment description to the Folk classification (43) and then converting the Folk classification to percentages based on the means in each category. In addition to analyses using covariates of *d* or *r*, we also conducted analyses using covariates of the *d/r* ratio; here, the *d/r* ratio was approximated as the ratio of *d* or *P* to the continuous *r* covariates. The effect of trawling is expected to increase with water depth owing to the lower levels of natural disturbance in deeper water and the corresponding increase in the relative abundance of individuals with slower life histories (low *r*), and therefore, $d \times$ depth was examined as a covariate for *d/r*, with depth expressed as a negative number.

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Supporting Information

Text S1. Elaboration of systematic review process

Data were collated from published experimental and comparative studies of the effects of bottom trawling on seabed habitat and biota following a systematic review protocol (1).

'Bottom trawling' is defined here to include any commercial towed bottom gear, including otter trawls, beam trawls, scallop dredges and hydraulic dredges used to catch fish and invertebrates living in, on or in close association with seabed habitats. For the systematic review we attempted to find every study in journal papers, book chapters and grey literature reports that reported the effect of bottom trawling on the state of seabed (benthic) taxa (species or higher taxonomic levels) and communities (biomass, abundance, taxon richness and diversity). Each identified study had to pass quality assurance criteria before associated data were included in our analysis (1). This approach eliminated the possibility of bias in selection of the studies. We included studies that reported the effect of bottom fishing activities (exposure) on marine benthic biota (subject) and compared this with effects of no exposure or less exposure to bottom fishing gear (comparator). Studies also had to report a measurable effect (or outcome, non–significant results were included) on at least one identified component of the benthic biota (and to report outcomes from two or more areas of the seabed subject to different intensities of fishing disturbance. Data on the state of benthic biota were extracted from figures, tables or text within publications. We only used studies reporting whole community biomass and/or abundance of macrofaunal invertebrates (infauna and/or epifauna). This includes all species that were effectively sampled, including scavenging species. If essential data were missing, incomplete or contained obvious errors, the lead author was contacted to request these data and these data were included in the analysis if received. 42% of contacted authors responded and provided the requested data, 13% responded but could not supply the requested data, and 44% of authors did not respond. Meta–data were also extracted for each study (including location, depth, gear type, habitat, Table S2 & S3).

Most existing knowledge about fishing impacts has been gained from experimental studies, where abundance of benthic biota is recorded before and after experimental trawling. These studies were used to quantify the direct depletion *d* (or mortality) caused by the pass of a trawl (SI Text S2 for details on the analysis of this data). Comparative (or 'gradient' or 'observational') studies are studies where the benthic community is compared over a gradient of two or more levels of quantified fishing effort, where trawling effort may have been continuous, seasonal or a single event (SI Text S3 for details on the analysis of these data). The comparative studies allow the estimation of the ratio of *d* to *r*, and estimation of *r* when *d* is known from the experimental studies.

Gear types in the studies were classified as otter trawls (OT), beam trawls (BT), towed dredges (TD) and hydraulic dredges (HD). Otter trawls are widely used in all types of fisheries on a wide range of sediments and target species like gadoids, some flatfishes and prawns. The use of beam trawls is more restricted to sandy and gravelly bottoms and these gears are mostly used to target flatfishes and shrimps. Towed dredges are generally used to target scallops or other bivalve molluscs, and are often fished on gravelly bottoms. Hydraulic dredges are used to target buried bivalves and resuspend sediment to a depth of up to 40 cm. They are often used in intertidal and other shallow areas (2, 3).

Text S2. Estimating depletion from experimental studies and penetration depth

Depletion *d* for macrofauna community biomass and abundance was estimated from the experimental studies identified in the systematic review. Studies used before–after (BA), control–impact (CI), or before–after–control–impact (BACI) designs. 13 of the studies were carried out in areas that were trawled in the last two years but generally at low intensity, 9 were carried out in areas that were last trawled between 10 and 25 years ago, and 10 were carried out in areas that have no fishing history. For the remaining studies this information was not given. Most experiments have therefore been conducted in infrequently trawled and untrawled areas, this is possible because even in the most heavily trawled areas like Europe about one-third of the seabed is not trawled (3). We used the log response ratio (*lnRR*) as the response variable, which was calculated as ln(response fished /response control) for CI studies and ln(response after/response before) for BA studies. The combined variance was calculated as in Borenstein et al. (4). For BACI studies, calculation of the *lnRR* and combined variance was more complicated. Let $y = \log X$ denote the log abundance and consider the four combinations of control/impact and before/after: y_{CB}, y_{CA}, y_{IB}, and y_{IA}. We assumed that effects are multiplicative on the abundance scale, and therefore are additive on the log scale. Let a be the before-after (period) effect, b the treatment effect, and c the interaction term. Then $y_{CB} = \mu$, $y_{CA} = \mu + a$, $y_{IB} = \mu + b$ and $y_{IA} = \mu + a + b + c$.

This means that $c = y_{IA} - y_{IB} - y_{CA} + y_{CB}$. On the abundance scale this implies

$$c = \log\left[\frac{X_{IA}}{X_{IB}} \Big/ \frac{X_{CA}}{X_{CB}}\right] \qquad \text{(eq S2.1)}$$

The quantity c is the analogue of $\ln\mathrm{RR}$ for BACI data. The variance calculation uses the following approximation:

$$\mathrm{Var}[\log X] \simeq \frac{\mathrm{Var}[X]}{[\mathrm{E}X]^2} \qquad \text{(eq S2.2)}$$

This leads to this expression for the variance

$$\mathrm{Var}[c] \simeq \frac{\mathrm{SD}_{IA}^2}{n_{IA}\overline{X}_{IA}^2} + \frac{\mathrm{SD}_{IB}^2}{n_{IB}\overline{X}_{IB}^2} + \frac{\mathrm{SD}_{CA}^2}{n_{CA}\overline{X}_{CA}^2} + \frac{\mathrm{SD}_{CB}^2}{n_{CB}\overline{X}_{CB}^2} \qquad \text{(eq S2.3)}$$

The *lnRR* will be more negative in areas that have been exposed to a higher frequency of fishing disturbance. Therefore, it was corrected using *lnRR* = $lnRR_{\text{uncorrected}}$/*Idis* where *Idis* is the number of trawl passes over the fished area.

The number of data points available for estimating *d* was limited: 55 for community biomass and 101 for community abundance (OT: 25, BT: 6, TD: 87, HD: 38). Including the response unit (biomass or abundance) as a factor in the model did not result in a lower AIC, therefore we estimated *d* using both biomass and abundance values in a single model.

Penetration depth of different gear types

Predicted penetration depth (*P*) of each trawl type was estimated from the penetration depth of the individual components of the gear weighted by the width of these components. Penetration depth is defined as the depth to which the sediment was disturbed by the fishing gear, but in practice often measured as the depth to which the sediment was excavated. We conducted a systematic search of the literature starting from Table 6 in Eigaard et al. (5). Each reference in the table was checked and only included when a study directly measured penetration depth. A database of experimental and comparative studies of fishing impacts, produced during a systematic review (1) was also screened for further studies that provided measurements of penetration depth. In addition, references cited within each reference already identified were screened and further studies included as a result. Any study for which penetration depth of a fishing gear (whole), or a gear component, was measured or inferred by one of the following methods was included: underwater video, underwater photographs side-scan sonar, sediment profile images, markers in sediment, observations by SCUBA divers, high resolution acoustic array, underwater laser, inferred from the living position of benthic organisms retained by the fishing gear, or in the case of intertidal fishing methods – by direct observation. Because different methods were used, estimates of penetration depths across studies may not be directly comparable, although they are the best available estimates. Review papers that were not the primary source of penetration depth data were not included, but were used to identify primary sources of data. Studies that reported penetration depths but that were not included in our analysis are given in Table S8.

The sources we identified reported the penetration depth either for the whole gear or for individual gear components (e.g., doors, sweeps, and bridles of an OT). The predicted penetration depth per gear component was therefore estimated by fitting a nested linear model where log(penetration+1) ~ sediment type + Gear|Component. Although we were not directly interested in the effect of sediment type, it was included because within gears the penetration seemed to vary with sediment type and it allowed us to correct for this effect in the final *P* estimates (Gear:Component $F_{9,74}$=6.57, p <0.001, Habitat $F_{3,71}$=2.6, p=0.057). We used the fitted model to predict the penetration depth for each gear component in each sediment type, and estimated the overall *P* for each fishing gear from this in two steps. We first averaged predicted penetration depths over all sediment types for each gear component, and then estimated the mean *P* for each gear by taking the mean weighted by the width of these components.

Text S3. Estimating the effect of trawling in comparative studies

As described in the main text, the responses from different studies were normalised to the common units of *B/K*. *K* was estimated for each of the sampling methods as 10^intercept of the relationship of $\log_{10} B$ versus *F*. In some studies the biota was sampled using two or more methods, each suited to sampling a different component of the community. For example, Hiddink et al. (6) sampled each station across a gradient of trawling frequency with an anchor dredge, box corer and 2m beam trawl. Where two or more sampling methods were used to sample benthic community biomass, *K* was estimated separately for each sampling gear. Studies were treated as replicate measurements by using study as a random effect.

A collective analysis of gradient studies requires fishing pressure to be described on a common scale. We adopted trawling frequency, *F* (y^{-1}), which is equivalent to the swept area ratio (km^2 km^{-2} y^{-1}). Trawling frequency expresses how often each cell is trawled i in a year, and is calculated by dividing the area trawled in a year by the area of the study site or other defined area (e.g. grid cell). Trawled area is usually calculated using logbook or vessel monitoring system (VMS) data, from the number of hours spent fishing multiplied by the fishing speed and the width of the fishing gear. Trawling frequency was explicitly reported for about half the comparative studies, and for the other half we calculated trawling frequency from the reported fishing effort (Table S9). Where trawling frequency could not be calculated, the study was excluded from further analyses.

Here we apply eq. 3.1 for estimating the effect of trawling on *B/K* for groups of species and communities. These communities, however, comprise many species with wide variety of *r* and *K* values. Therefore, the response to fishing is the sum of the responses of all those species. Because low–*r* species will be more depleted than high–*r* species, and will potentially be extirpated from the community, the response of the community to *F* is not a straight line as in eq. 3.1. Consequently, the average *r* of the community increases with *F*, and the marginal effect of each additional unit of *F* on community *B*/*K* decreases with increasing *F*. We simulated a community of species by drawing *r* and *K* values at random, and found that the resulting relationship between total community *B* and *F* is well approximated by a log–linear relationship for normal and exponential distributions of *r* and *K*. We therefore estimated the effect of trawling on communities by fitting a model based on the approximation:

$\log_{10}(B/K) \sim bF$ (eq. S3.1)

where b is the slope of the relationship. After fitting a linear relationship to $\log_{10} B$ versus F for each comparative study, K was estimated as the $10^{\text{intercept}}$ of this relationship.

Text S4. Estimating *r* from *d* and *b* and quantifying uncertainty

Comparative studies involve sampling the seabed biota at locations within sites subject to different frequencies of trawling disturbance. Collectively, the sampling locations only cover a small proportion of each site, but the mean trawling frequency estimated for the site is assumed to apply to all stations within the site because data on trawl positions are not sufficiently resolved to estimate location-specific trawling frequency. Thus samples linked to the same mean trawling frequency for the site may come from heavily trawled patches, lightly trawled patches, and potentially some untrawled patches, within the site. Consequently, the mean recovery rate estimated for the site (*R*) will not be the same as the intrinsic rate of recovery *r* in equation (1). If the distribution which describes the patchiness of trawling within a site is known then *r* can be estimated following the approach in Ellis et al. (7). Given that $\log_{10}(B/K) \sim bF$ (SI Text S3) and that $B/K = 1-(d/R)\,F$, it follows that $10^{bF} = 1-(d/R)\,F$. The equation to estimate *R* from *r* for a single species in Ellis et al. (7, R = r log(1+βd)/[-β log(1-d)]) can therefore be rewritten to estimate *r* for the community as:

$$r = R \Big/ \frac{\log(1+\beta d)}{-\beta\,\log(1-d)} \qquad \text{(eq S4.1)}$$

where

$$R = \frac{-d}{(10^{b\,F}-1)\,/F} \qquad \text{(eq S4.2)}$$

where β is a parameter defining the spatial distribution of trawling within a site (7). Here we assumed β ≈ 0, representing a random distribution of trawling within a site (in practice $\beta = 10^{-6}$ because the equation is undefined when β = 0). A random distribution within sites is supported by data on the spatial distribution of trawling collected at scales of around 1 km and smaller (8), consistent with the scales at which sites in comparative trawling studies are defined. Assuming a uniform distribution of trawling (β = –1) resulted in *r* estimates that were approximately 10% lower. Equation S4.1 and S4.2 indicate that *r* depends on *F*, which is expected because changes in community composition to favour biota with faster life histories. Because we aim to estimate recovery rates and times for the original unfished community, we used estimates of *r* at *F* = 0 to estimate recovery times. If the distribution of trawling in a cell is random, the site level depletion is the same as local depletion *d* and no correction was therefore applied here.

To propagate the uncertainty in the estimates of *b* and *d* into the estimate of *r* we sampled the distributions of *b* and *d* estimates to derive the distribution of *r*. The value of *b* was taken as negative and –*b* was assumed to have a log-normal distribution, with the standard deviation estimated from the distribution of the random slopes using the *fitdist* function in the *fitdistrplus* package in R (9). The value of *d* was assumed to be positive and bounded between 0 and 1, and to have a logitnormal distribution with standard deviation estimated with the function *twCoefLogitnorm* of the *logitnorm* package in R (10). We sampled 2000 combinations from the distributions of *b* and *d* to estimate the distribution of *r*.

Text S5. Estimating recovery time from *r*

The logistic *r* can be used to estimate recovery time (i.e. *T* from a defined level of depletion below *K* to a defined proportion of *K*). Lambert et al. (11) derived the recovery time *T* to 0.9*K* as:

$$T = \frac{1}{\mathrm{r}}[\ln\left(\frac{0.9K}{B_{t=o}}\right) + \ln\left(\frac{K - B_{t=o}}{0.1K}\right)] \qquad \text{(eq. S5.1)}$$

If we generalise this in terms of any fraction of *K* at which recovery is deemed to have occurred (ϕ) and assume that $B_{t=0}$ is the biomass or abundance of an unimpacted habitat remaining after the pass of a gear that reduces biomass or abundance by a fraction *d*, then the recovery time given these conditions would be:

$$T = \frac{1}{\mathrm{r}}[\ln\left(\frac{\phi K}{K(1-d)}\right) + \ln\left(\frac{K - K(1-d)}{K(1-\phi)}\right)] \qquad \text{(eq. S5.2)}$$

which can be expressed more simply as:

$$T = \frac{1}{\mathrm{r}}\ln\left(\frac{\phi \mathrm{d}}{(1-d)(1-\phi)}\right) \qquad \text{(eq. S5.3)}$$

Table S1. Number of studies of whole community biomass and abundance for macrofauna per gear and habitat. Otter trawls (OT), beam trawls (BT), towed dredges (TD), hydraulic dredges (HD).

a) Experimental studies

	OT	BT	TD	HD
Biogenic	–	–	–	–
Gravel	1	–	1	–
Sand	6	4	16	10
Sandy mud/Muddy sand	–	–	–	2
Mud	5	–	–	1

b) Comparative studies

	OT	BT	TD	HD
Biogenic	–	–	–	–
Gravel	1	–	5	–
Sand	3	4	–	–
Sandy mud/Muddy sand	5	2	–	–
Mud	4	–	–	–

Table S2. Metadata for included experimental studies. A single paper is listed more than once when two or more studies were reported in the same paper.

Source	Region	Habitat	Depth (m)	Gear
(12)	Southern Europe	S	8	TD
(12)	Southern Europe	S	8	TD
(13)	Alaska	S	25	OT
(14)	Southern Europe	S	9	TD
(14)	Southern Europe	S	9	TD
(15)	Southern Europe	S	6	TD
(15)	Southern Europe	S	18	TD
(16)	Australia	S	20	OT
(16)	Australia	M	18	OT
(16)	Australia	S	20	OT
(17)	Northern Europe	S	10	TD
(17)	Northern Europe	S	10	TD
(17)	Northern Europe	S	10	TD
(17)	Northern Europe	S	10	TD
(18)	North America	mS	65	HD
(19)	North America	S	5.5	HD
(20)	Northern Europe	mS	0	HD
(21)	Northern Europe	S	7	HD
(22)	North America	G	70	OT
(23)	Northern Europe	S	21.5	TD
(23)	Northern Europe	S	21.5	OT
(23)	Northern Europe	S	21.5	TD
(24)	Northern Europe	S	26	BT
(24)	Northern Europe	S	34	BT
(25)	Northern Europe	S	0	HD
(26)	Northern Europe	S	30	BT
(26)	Northern Europe	S	30	BT
(27)	North America	S	0.2	HD
(27)	North America	S	0.2	HD
(27)	North America	S	0.2	HD
(28)	Southern Europe	S	24	TD

(29)	Southern Europe	S	23	TD
(29)	Southern Europe	M	11	TD
(30)	South America	S	10	OT
(31)	Canada	S	133	OT
(32)	Southern Europe	M	30	OT
(32)	Southern Europe	M	40	OT
(33)	Australia	S	0	HD
(34)	North America	M	61	OT
(35)	Northern Europe	M	0	HD
(36)	New Zealand	S	24	TD
(37)	New Zealand	S	24	TD
(38)	Northern Europe	M	33.5	OT
(39)	Northern Europe	S	3.5	HD
(40)	South Africa	S	0	HD
(40)	South Africa	S	0	HD

Table S3. Metadata for included comparative studies. sM & mS – sandy mud and muddy sand.

Source	Region	Habitat	Depth (m)	Gear
(41)	South Africa	sM & mS	420	OT
(42)	Eastern North America	Gravel	48	TD
(43)	South Coast Australia	Sand	30	OT
(44)	North Sea	Mud	80	OT
(6)	North Sea	Sand	32.5	BT
(6)	North Sea	Sand	40	BT
(45)	Northwest Europe	sM & mS	31.5	OT
(46)	North west Europe	sM & mS	31.5	OT
(47)	Central North Sea,	sM & mS	57.5	BT
(47)	Central North Sea,	Sand	57.5	BT
(48)	North Sea	sM & mS	50	BT
(49)	Irish Sea	Gravel	43.5	TD
(50)	Mediterranean Sea	Mud	137.145	OT
(51, 52)*	Australia	sM & mS	27.5	OT
(51, 52)*	Australia	Sand	25.5	OT
(53)	Irish Sea	sM & mS	30	OT
(54)	North West Europe	Sand	40	BT
(55)	Eastern North America	Gravel	74	TD
(55)	Eastern North America	Gravel	50	TD
(56)	Australia	Sand	23.5	OT
(57)	North west Europe	Mud	147.5	OT
(57)	North west Europe	Gravel	78.5	OT
(58)	Irish Sea	Gravel	43.5	TD
(59)	North west Europe	Mud	100	OT

* sources combined

Table S4. Penetration depth *P* and depletion *d* of community biomass and abundance for different trawling gears. The 5 and 95% percentiles for *d* estimates are given. Gear types are otter trawls (OT), beam trawls (BT), towed dredges (TD) and hydraulic dredges (HD).

Gear	Penetration depth (cm)			Depletion *d* (fraction)		
	mean	±	sd	5%	Median	95%
OT	2.44	±	1.14	0.02	0.06	0.16
BT	2.72	±	1.24	0.07	0.14	0.25
TD	5.47	±	2.19	0.13	0.20	0.30
HD	16.11	±	5.80	0.35	0.41	0.48

Table S5. AIC estimates of the linear mixed models with different explanatory variables for community biomass and abundance in comparative studies. The model with the lowest AIC for biomass and the two models with the lowest AIC for abundance are given in bold.

Model	Biomass	Abundance
None	**566.9**	89.5
Habitat	573.1	94.3
Gear	572.5	92.4
d	568.9	89.5
Penetration	568.8	89.3
SBT	568.8	89.1
Depth	567.7	91.4
POC	567.7	91.1
PP	568.0	90.9
Gravel	568.4	**81.1**
Sand	568.8	89.2
Mud	568.9	90.2
d/SBT	568.9	89.5
*d**Depth	567.9	90.8
d/POC	568.7	91.1
d/PP	568.8	**86.1**
Penetration/SBT	568.9	90.0
Penetration×Depth	567.8	91.4
Penetration/POC	568.5	91.4
Penetration/PP	568.7	89.0

d = depletion estimate from experimental studies (fraction per trawl pass)

Penetration = penetration depth of fishing gear into the seabed (cm)

SBT = sea bottom temperature (°C)

POC = Particulate organic carbon flux to the seabed (g C_{org} m^{-2} yr^{-1})

PP = Primary production (mg C m^{-2} d^{-1})

Gravel, Sand & Mud = sediment composition in % by weight

Habitat = categorical variable with levels Mud, sM & mS, Sand and Gravel.

Table S6. Parameters used to estimate *r* and percentiles from the distribution of *r* estimates. SD = standard deviation. SAR= swept area ratio.

	Biomass	**Abundance**		
Gear type	Combined	OT	BT	TD
Gravel content (%)	NA	0.84	0.00	44.63
d (fraction)	0.13	0.06	0.14	0.20
SD of *d*	0.08	0.08	0.08	0.08
b (slope)	-0.075	-0.025	-0.015	-0.553
SD of *b*	0.003	0.057	0.057	0.057
% decline with unit increase in SAR	15.90	5.50	3.29	71.99
Recovery time from 0.5*K* to 0.95*K* (years, using median *r*)	3.58	2.81	0.66	16.65
r, 5% percentile	0.42	0.33	2.37	0.11
r, 10% percentile	0.49	0.43	2.75	0.12
r, 25% percentile	0.63	0.66	3.50	0.15
r, 50% percenttile	0.82	1.05	4.49	0.18
r, 75% percentile	1.06	1.66	5.71	0.21
r, 90% percentile	1.34	2.60	7.18	0.25
r, 95% percentile	1.54	3.54	8.21	0.28

Table S7. Studies used to estimate the penetration depth of different gear types. Weighting is the fraction of the width of the gear occupied by a component.

Source	Gear	Component	Habitat	Penetration (cm)	Weighting
(60)	BT	Beam trawl - whole gear	Sand	6	1
(61)	BT	Beam trawl - whole gear	Sand	2.26	1
(61)	BT	Beam trawl - whole gear	Mud	5.29	1
(62)	BT	Beam trawl - whole gear	Sand	1	1
(63)	BT	Beam trawl - tickler chains	Mud	1.4	0.94
(64)	BT	Beam trawl - tickler chains	Sand	0.75	0.94
(65)	BT	Beam trawl - tickler chains	Sand	6	0.94
(63)	BT	Beam trawl - tickler chains	Sand	0.4	0.94
(63)	BT	Beam trawl - tickler chains	Gravel	0.5	0.94
(64)	BT	Beam trawl - tickler chains	Mud	0.9	0.94
(61)	BT	Beam trawl - tickler chains	Sand	1	0.94
(64)	BT	Beam trawl - tickler chains	Sand	0	0.94
(61)	BT	Beam trawl - trawl shoes	Sand	1.9	0.06
(64)	BT	Beam trawl - trawl shoes	Sand	1.5	0.06
(66)	OT	Otter trawl - whole gear	Mud	8.5	1
(67)	OT	Otter trawl - whole gear	Sand	4.5	1
(66)	OT	Otter trawl - whole gear	Sand	0.085	1
(68)	OT	Otter trawl - whole gear	Gravel	4.5	1
(69)	OT	Otter trawl - sweeps	Mud	2.18	0.73
(69)	OT	Otter trawl - ground gear	Mud	1.4	0.25
(70)	OT	Otter trawl - ground gear	Mud	0	0.25
(71)	OT	Otter trawl - trawl doors	Mud	30	0.02
(72)	OT	Otter trawl - trawl doors	Mud	12.5	0.02
(73)	OT	Otter trawl - trawl doors	Mud	5.5	0.02
(73)	OT	Otter trawl - trawl doors	Sand	2.7	0.02
(69)	OT	Otter trawl - trawl doors	Mud	6.43	0.02
(71)	OT	Otter trawl - trawl doors	Sand	20	0.02
(72)	OT	Otter trawl - trawl doors	Sand	2.5	0.02
(74)	OT	Otter trawl - trawl doors	Sand	10	0.02
(75)	OT	Otter trawl - trawl doors	Mud	5	0.02
(75)	OT	Otter trawl - trawl doors	Sand	2.5	0.02
(69)	OT	Otter trawl - trawl doors	Sand	0.26	0.02
(69)	OT	Otter trawl - trawl doors	Sand	2.1	0.02

(69)	OT	Otter trawl - trawl doors	Sand	5.8	0.02
(69)	OT	Otter trawl - trawl doors	Sand	0.2	0.02
(76)	OT	Otter trawl - trawl doors	Gravel	5.5	0.02
(77)	OT	Otter trawl - trawl doors	Sand	15	0.02
(62)	OT	Otter trawl - trawl doors	Mud	14	0.02
(70)	OT	Otter trawl - trawl doors	Mud	4.5	0.02
(75)	OT	Twin Otter trawl - roller clump	Sand	0	0.01
(75)	OT	Twin Otter trawl - roller clump	Mud	0	0.01
(72)	OT	Twin Otter trawl - roller clump	Mud	3.5	0.01
(73)	OT	Twin Otter trawl - roller clump	Mud	12.5	0.01
(76)	OT	Twin Otter trawl - roller clump	Mud	12	0.01
(73)	OT	Twin Otter trawl - roller clump	Sand	3.65	0.01
(66)	OT	Otter trawl - whole gear	Mud	8.5	1
(67)	OT	Otter trawl - whole gear	Sand	4.5	1
(66)	OT	Otter trawl - whole gear	Sand	0.085	1
(68)	OT	Otter trawl - whole gear	Gravel	4.5	1
(69)	OT	Otter trawl - sweeps	Mud	2.18	0.73
(69)	OT	Otter trawl - ground gear	Mud	1.4	0.25
(70)	OT	Otter trawl - ground gear	Mud	0	0.25
(71)	OT	Otter trawl - trawl doors	Mud	30	0.01
(72)	OT	Otter trawl - trawl doors	Mud	12.5	0.01
(73)	OT	Otter trawl - trawl doors	Mud	5.5	0.01
(73)	OT	Otter trawl - trawl doors	Sand	2.7	0.01
(69)	OT	Otter trawl - trawl doors	Mud	6.43	0.01
(71)	OT	Otter trawl - trawl doors	Sand	20	0.01
(72)	OT	Otter trawl - trawl doors	Sand	2.5	0.01
(74)	OT	Otter trawl - trawl doors	Sand	10	0.01
(75)	OT	Otter trawl - trawl doors	Mud	5	0.01
(75)	OT	Otter trawl - trawl doors	Sand	2.5	0.01
(69)	OT	Otter trawl - trawl doors	Sand	0.26	0.01
(69)	OT	Otter trawl - trawl doors	Sand	2.1	0.01
(69)	OT	Otter trawl - trawl doors	Sand	5.8	0.01
(69)	OT	Otter trawl - trawl doors	Sand	0.2	0.01
(76)	OT	Otter trawl - trawl doors	Gravel	5.5	0.01
(77)	OT	Otter trawl - trawl doors	Sand	15	0.01
(62)	OT	Otter trawl - trawl doors	Mud	14	0.01
(70)	OT	Otter trawl - trawl doors	Mud	4.5	0.01
(35)	HD	Hydraulic dredge	Mud	10	1

(18)	HD	Hydraulic dredge	Sand	20	1
(19)	HD	Hydraulic dredge	Sand	5	1
(20)	HD	Hydraulic dredge	Mud	30	1
(21)	HD	Hydraulic dredge	Sand	25	1
(25)	HD	Hydraulic dredge	Mud	10	1
(78)	HD	Hydraulic dredge	Sand	9	1
(79)	HD	Hydraulic dredge	Sand	40	1
(20)	HD	Tractor dredge	Mud	30	1
(80)	HD	Hydraulic dredge	Sand	5	1
(28)	TD	Boat Dredge - whole gear	Sand	6	1
(17)	TD	Boat Dredge - teeth	Sand	3.5	1
(81)	TD	Boat Dredge - teeth	Maerl	10	1
(82)	TD	Boat Dredge - whole gear	Sand	2.5	1
(82)	TD	Boat Dredge - whole gear	Gravel	3.5	1
(82)	TD	Boat Dredge - whole gear	Gravel	5.9	1

Table S8. A list of studies which relate to the physical impacts of towed-bottom fishing gears, but were not included in the penetration depth calculations for the reasons given.

Source	Reason for non-inclusion
(83)	Not the primary source of the reported gear penetration depth
(84)	Penetration depth not reported
(85)	Penetration depth not reported
(86)	Penetration depth not reported
(87)	Review paper, therefore not a primary data source
(88)	Penetration depths obtained from a numerical model, rather than direct measurements
(89)	Penetration depth not reported
(90)	Not the primary source of the reported gear penetration depth
(91)	Not the primary source of the reported gear penetration depth
(92)	Unable to obtain manuscript, however a penetration depth of c. 6.5cm is cited in de Groot (1995) and referenced to this report.
(93)	Not the primary source of the reported gear penetration depth
(94)	The source of the seabed marks measured in the study is ambiguous
(95, 96)	Penetration depth inferred from amount of suspended sediment only, missing non-suspended component of penetration.

Table S9. Trawling frequency calculations for comparative studies where trawling frequency was not reported as the swept area ratio (SAR).

Paper	Region	Habitat	Depth (m)	Gear	Gear	Source of swept area ratio estimate (SA)	Reported effort	Area box	Fishing speed	Gear width (m)	SAR calculation (after converting to the same units)	Min SAR (y^{-1})	Max SAR (y^{-1})
Abbreviation							**E**	**A**	**Sp**	**W**			
Collie et al. 2005	Georges Bank, North America	Gravel	48	Scallop dredge	TD	Calculated	hrs fished y^{-1}	1 nm^2	3 kn	8	E*Sp*W/A	0.0	3.7
Currie et al. 2011	Spencer Gulf , South Eastern Australia	Sand	30	Prawn trawl	OT	Calculated	h km^{-2}		3 kn	29.26	E*Sp*W	0.1	2.9
Frid et al. 1999	Northumberland, NE England, USA	Mud	80	Otter trawls	OT	Calculated	km^2 trawled y^{-1}	ICES††			E/A	0.0	12.9
Jennings et al. 2001a	Silver Pit, North Sea	Sm & Ms	57.5	Beam trawl	BT	Estimated using VMS						0.5	5.4
Jennings et al. 2001b	Hills, North Sea	Sand	57.5	Beam trawl	BT	Estimated using VMS						0.1	2.3
Jennings et al. 2002	Silver Pit, North Sea	Sm & Ms	50	Beam and otter trawls	BT	Estimated using VMS						0.4	5.0
Kaiser et al.	Irish Sea, Isle of	Gravel	43.5	Scallop	TD	Calculate	hrs fished	5x5 nm	2.5 kn	12.0†	E*Sp*W/A	0.1	3.2

2000b	Man			dredge		d	y^{-1}						
Reiss et al. 2009	German Bight, Germany	Sand	40	Beam trawl	BT	Reported						0.1	2.0
Smith et al. 2013a	North East Peak, Georges Bank, N. America	Gravel	74	Scallop dredge	TD	Calculated	hrs fished y^{-1}	50 km^2	3 kn	30	E*Sp*W/A	0.0	0.4
Smith et al. 2013b	CAI, Georges Bank, N. America	Gravel	50	Scallop dredge	TD	Calculated	hrs fished y^{-1}	50 km^2	3 kn	30	E*Sp*W/A	0.0	0.4
Svane et al. 2009	Spencer Gulf, Australia	Sand	23.5	Prawn trawl	OT	Calculated	h trawled per year	645 to 1128 km2	2.5 kn	29.26	E*Sp*W/A	0.2	1.9
Veale et al. 2000	Irish Sea, Isle of Man	Gravel	43.5	Scallop dredge	TD	Calculated	m x h y^{-1}	5x5 nm	2.5 kn	10	E*Sp*W/A	0.0	1.7
Vergnon & Blanchard 2006	Grande Vasiere, Bay of Biscay, France	Mud	100	Nephrops trawl	OT	Calculated	mths fished y^{-1}	ICES rectangle (1 * 0.5 degree)	2 kn	10	E*Sp*W/A	1.6	7.9

† 16 dredges (10 within 3nmi limit) of 0.75m width.

†† ICES rectangles of size 1° × 0.5°.

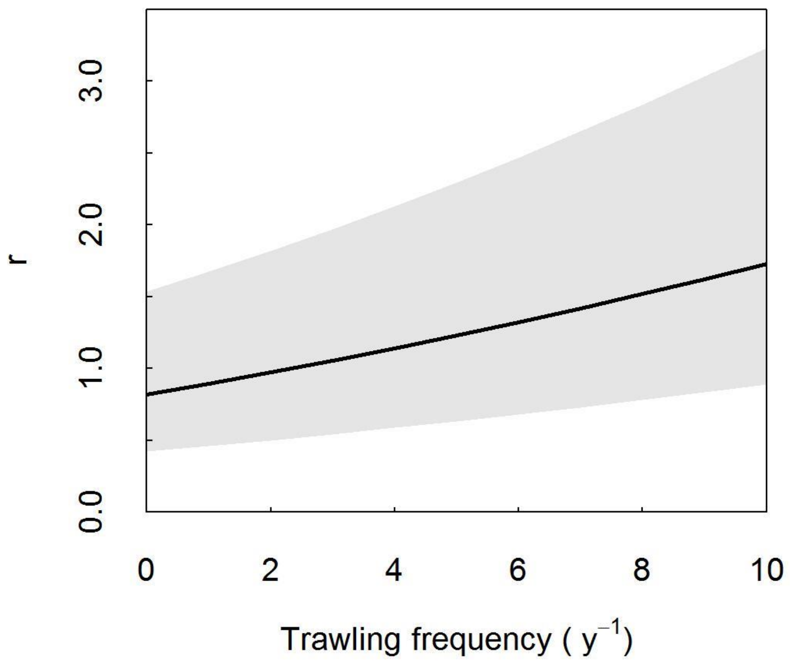

Figure S1. Predicted increase in median r (±5-95% quantiles) with trawling frequency for community biomass, as estimated from the relationship between $\log_{10}B/K$ and trawling frequency (equations S4.1 and S4.2). Simulation assumes mean value of d over all fishing gears included in the comparative studies (d = 0.13).

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